Bone-related behaviours of captive chimpanzees (*Pan troglodytes*) during an excavating experiment

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After stone tools, bone tools are the most abundant artefact type in the Early Pleistocene archaeological record. That said, they are still relatively scarce, limiting our understanding of the behaviors that led to their production and use. Observations of extant primates constitute a unique source of behavioural data with which to construct hypotheses about the potential uses of bone tools by our ancient hominin ancestors. In this study, we investigated the behavioural responses of two groups of captive chimpanzees (*Pan troglodytes*) (Ntotal=42) to the availability of disarticulated, defleshed, ungulate bones while participating in a foraging task aimed at eliciting excavating behavior involving those same bone specimens. Each chimpanzee group was provided with bone specimens of different characteristics and the two groups differed in their respective levels of experience with using tools to excavate (one group was mostly inexperienced while the other had ample experience utilizing sticks as excavating tools). We found that several individuals from the inexperienced group used the provided bone specimens as tools during the task. In contrast, none of the individuals from the experienced group used bones as excavating tools. Instead, these experienced chimpanzees performed other bone-related behaviours (not observed in the inexperienced group), such as hammering and extracting marrow with wooden tools. Given that previous experience in tool excavation did not predict the use of bones as tools in the excavating task, we hypothesize that the differences in behavior observed between the two chimpanzee groups were the result of the varying characteristics of the bones provided to each. Furthermore, our results suggest that it is the intrinsic characteristics of raw materials rather than the material itself that determines whether chimpanzees perceive an object as a suitable excavating tool.

Keywords: bone tools, chimpanzees, tool-assisted excavation, tool properties

Introduction

Early hominin technological artefacts found in the archaeological record include tools made from different raw materials, such as multiple rock types (e.g. basalt, flint, obsidian) and bone (reviewed by Toth & Schick, 2015). Bone tools have been found in Early Pleistocene archaeological sites across the Old World (reviewed by Backwell & d’Errico, 2014). For instance, the manufacture and use of bone tools by early African hominins, including possibly the genera *Paranthropus* and *Homo*, have been established through the identification of anthropogenically derived modification of the shapes and surface textures of ungulate bone fragments from sites such as Swartkrans, Drimolen, Sterkfontein, and Kromdraai, in South Africa (Backwell et al., 2008; Brain & Sillent, 1988; Robinson, 1959; Stammers et al., 2018), and Olduvai Gorge, in Tanzania (Leakey, 1971). To date, the function(s) of these early bone tools remains contested, but most studies agree that they were probably used at least occasionally for digging activities of some sort that were likely related to foraging (Backwell & d’Errico, 2001, 2005; Brain & Shipman, 1993).

Regardless of the precise use(s) for which early hominins employed bone tools, a necessary first step in the development of any technology—including bone technology—is the identification of a particular raw material as a potential tool source. Several hypotheses have been proposed to explain the emergence of technological innovations (e.g. Fox et al., 1999, 2004; Gruber et al., 2016; Grund et al., 2019), all of which highlight the role that environmental factors play in the emergence of tool behaviours. The necessity hypothesis postulates that tool

innovations are linked to caloric needs and thus often take place during periods of food scarcity where preferred, easily accessible food items become unavailable (Moura & Lee, 2004; Yamakoshi, 1998). In such situations, individuals of certain species turn to tool use as a mean to access highly caloric but costly (i.e., in terms of foraging time and effort) resources such as encased foods (e.g. nuts, Moura & Lee, 2004), insects protected by architectural structures (e.g. termites) or underground foods (e.g. honey, Gruber et al., 2016). Alternatively, the opportunity hypothesis postulates that tool use emerges as a consequence of chance encounters with, for example, potential raw materials that are suitable for tool manufacture (Fox et al., 2004; Koops et al., 2013). A third hypothesis, the relative profitability hypothesis, stipulates that tool use emerges as a response to a caloric need when using tools is more efficient than is not using tools (Rutz & St Clair, 2012). Varying degrees of support have been found for these hypotheses in explaining how and why some populations of nonhuman great apes (henceforth apes) develop or do not develop specific tool-using behaviors (Fox et al., 2004; Gruber et al., 2016; Koops et al., 2013; Sanz & Morgan, 2013). If apes are assumed to represent valid phylogenetic models for early hominin behaviour (Carvalho & McGrew, 2012; Rolian & Carvalho, 2017; Wynn et al., 2011), then similar ecological pressures to those described for apes could have played a role in the initial emergence and/or maintenance of early hominin bone technologies.

To date, two experimental studies tested the use of skeletal materials as tools by nonhuman primates. Westergaard and Suomi (1994) investigated whether nine captive capuchin monkeys (*Sapajus apella*) could spontaneously – in the absence of demonstrations – use bovid limb fragments as pounding tools in order to crack open

nuts and/or as cutting tools to open a puzzle box baited with food. The authors found that the same three monkeys out of the nine tested spontaneously performed both tasks. In addition, Roffman et al. (2015) assessed whether bonobos (*Pan paniscus*) would use cervid antlers (and other raw materials) spontaneously as excavating tools in the absence of demonstrations. The authors found that captive bonobos from two different groups employed antlers as well as plant tools to excavate for buried food items.

Currently, the spontaneous bone tool-using abilities of chimpanzees (*Pan troglodytes*)—the closet living relative of modern humans and the ape species with the broadest tool repertoire in the animal kingdom—remains unknown. Chimpanzees are known to use a wide variety of tools flexibly, as well as to select appropriate tools for specific tasks, and thus show an understanding of tool material properties (Lamon et al., 2018; Manrique et al., 2010; Sakura & Matsuzawa, 1991; Sirianni et al., 2015). However, no study to date has investigated whether untrained captive chimpanzees can identify and use bones as tools—a skill that must have necessarily preceded the emergence of bone technologies in our lineage. More generally, chimpanzees in captivity have rarely been presented with disarticulated bones. Wynn & McGrew (1989: 387), citing Kithara-Frisch et al. (1987; in Japanese), report that “chimpanzees shown how to use hammer-stones to smash long-bones then used the resulting bone fragments to puncture a skin covering a bottle of sweetened drink.” In a second bone-related study, Pickering & Wallis (1997) provided four groups of captive chimpanzees with the disarticulated bones of bovids and cervids, which were cleaned of adhering soft tissues and then coated with foods found palatable by the subjects. The goal of the study was to investigate the bone surface modifications inflicted by

the teeth of chimpanzees as they gnaw and chewed the bone coatings. In the wild, chimpanzees hunt a variety of small and medium-sized vertebrates (reviewed by Newton-Fisher, 2007), sometimes with the assistance of wooden tools (Pruetz & Bertolani, 2007). They also scavenge vertebrate carcasses (Watts, 2008), and have been reported to consume bone marrow with the aid of plant tools (Boesch & Boesch, 1990; Sanz & Morgan, 2007). However, there are no reports of the use of bone tools by wild chimpanzees.

In this study we focused on a behaviour that some authors have deemed crucial for the evolution of our species, namely tool-assisted excavation of edible underground resources (Laden & Wrangham, 2005). Tool-assisted foraging excavation has been described in both wild (Hernandez-Aguilar et al., 2007) and captive (Motes-Rodrigo et al., 2019) chimpanzees. In our lineage, this behaviour is present in modern humans (Lee, 1979) and in the past might have involved the use of bone tools (Brain & Shipman, 1993, see above). We conducted two experiments with two captive populations of chimpanzees that vary in their degree of excavating experience to investigate whether chimpanzees would recognize bones as potential excavating tools. Each population was provided with several defleshed, disarticulated bones or fragments that could be used as excavating tools to obtain buried food items. An experimental set up aimed at eliciting tool excavation was employed. The aims of our experiment were i) to describe the behavioural responses of captive chimpanzees to disarticulated bones, ii) to assess whether chimpanzees could identify (and use) bones as tools in order to excavate, ii) to assess whether the physical characteristics (e.g. dimensions and morphology) of the bones influenced the excavating or general tool-

use activity of the chimpanzees, and iii) to describe the excavating actions performed by the chimpanzees using the bones.

Materials and Methods

Study site and subjects

We studied two groups of captive chimpanzees housed at two different zoological institutions. The first group of chimpanzees is housed at Kristiansand Zoo, Norway, and consists of nine individuals (four adult males, four adult females, and one five-year old juvenile female). All chimpanzees were born in captivity and each but one chimpanzee was reared by its mother. The chimpanzees have access to both an indoor and an outdoor enclosure, as well as to individual sleeping rooms. The outdoor enclosure (1840 m²) is a forested island with natural soil, rocks, and vegetation, surrounded by a water-filled moat. Bedding material and structural enrichment such as logs, ropes, platforms and climbing structures are present both in the indoor and outdoor enclosures. In addition, several devices aimed at promoting the use of tools such as a puzzle box (i.e., nut maze) and several foraging enrichment devices (i.e. artificial termite mount and perforated hanging log) were available in the indoor enclosure and baited regularly. The chimpanzees were also often provided with other enrichment elements such as hose fragments, tubes and plastic bottles baited with preferred foods such as honey, yogurt and fruit smoothies. These preferred foods could be obtained using tools that the chimpanzees manufactured from leafy branches provided every day in the indoor enclosure. Consequently, the chimpanzees at Kristiansand Zoo manufactured and used plant tools on a daily basis in order to forage both from the fixed and mobile enrichment devices.

The second chimpanzee group is housed in Leintal Zoo in Schwaigern, Germany, and consisted of 33 chimpanzees (16 males, 17 females) ranging in age from 5 to 47 years (mean=22.4±1.58 years) at the time of testing. All chimpanzees were mother reared except for eight chimpanzees who were hand-reared by the zoo staff during varying periods of time. The chimpanzees have access to an indoor (329.82 m²), an outdoor enclosure (958.25 m²) and several sleeping rooms out of sight of the visitors. Bedding material and structural enrichment such as logs, ropes, platforms and climbing structures were present both in the indoor and outdoor enclosures. The outdoor enclosure consists of four interconnected areas surrounded by a metallic mesh 4 m high that limits the enclosure sidewise and from the top, acting as a roof. The floor of the outdoor enclosure is natural dirt. The tool use repertoire of the chimpanzees was limited to using sticks to attract the attention of the keepers (e.g. poke) and to rake food closer to the fence when food was placed in the vicinity of the outdoor enclosure during feedings. The chimpanzees were often provided with scattered seeds and nuts in the outdoor enclosure as foraging enrichment.

The chimpanzees at Kristiansand Zoo had previously participated in an excavating experiment where buried food items, as well as potential plant tools, were presented to the group in their outdoor enclosure (for details see Experiment 1 in Motes-Rodrigo et al., 2019). Thus, the chimpanzees at Kristiansand Zoo were familiar with excavating tools and all but one chimpanzee had previously engaged in tool-assisted excavation (Motes-Rodrigo et al., 2019). Prior to the start of the current experiments, the chimpanzee keepers at both institutions confirmed that none of the chimpanzees had any previous experienced with bones, including disarticulated and defleshed bones. The chimpanzee keepers at Leintal Zoo were interviewed regarding the

previous experience or exposure of the chimpanzees to excavation of any kind. These keepers reported that some of the chimpanzees (it was not noted which of them) had anecdotal experience with underground items (e.g. insects, baited bottles). Detailed descriptions of these reports can be found in the supplementary material.

Experimental design

Data were collected at Kristiansand Zoo during May and June 2016 and at Leintal Zoo from the 3rd to the 10th of October 2018. Three experimental conditions were implemented in each zoo following the protocol described by Motes-Rodrigo et al. (2019). Before the first experimental condition, the experimenter dug five holes in the outdoor enclosure of the chimpanzees while the chimpanzees were away in the indoor enclosure and were thus unable to observe the experimenter. The holes were 30 cm deep and 15 cm in diameter, following the dimensions of holes excavated by wild chimpanzees in Issa, Tanzania (Hernandez-Aguilar et al., 2007).

The first experimental condition (*Open holes condition*) comprised two sessions at Kristiansand Zoo and, due to time constraints, one session at Leintal Zoo. During the *Open holes condition*, the holes were left uncovered and a whole, previously washed food reward was placed inside each hole (grapes at Kristiansand and apples at Leintal). The aim of the *Open holes condition* was to attract the Kristiansand chimpanzees to the study area (as they were already familiar with buried items, Experiment 1 in Motes-Rodrigo et al., 2019) and to familiarize the Leintal chimpanzees with the presence of food within the holes in the study area. The second experimental condition (*Loose soil condition*) took place over two sessions at Kristiansand Zoo and one session at Leintal Zoo. For the *Loose soil condition*, we

placed a food reward inside of each hole but this time covered each hole with natural loose soil from the outdoor enclosure. The aim of this condition was to remind the Kristiansand chimpanzees of the testing procedure and to familiarize the Leintal chimpanzees with the presence of food hidden under soil. In sum, the two first conditions constituted a phase of familiarization for the chimpanzees with the experimental set-up. In Kristiansand Zoo the study area could only be accessed in the morning before the chimpanzees left their sleeping quarters, and thus, each experimental session lasted one entire day. In Leintal Zoo, the sessions of the *Open holes condition* and the *Loose soil condition* lasted two hours each (from 9 am to 11 am) as the chimpanzees could be moved out of the study area by the keepers during the day.

After the familiarization phase, we conducted the *Compacted soil condition* for a total of 16 days at Kristiansand Zoo and during six days at Leintal Zoo. During the *Compacted soil condition*, a fruit reward was placed inside each of the holes in the study area and each hole was then filled with compacted natural soil from the outdoor enclosure. Experimenters used their bodyweight to compact the soil first tamping it by hand and then stomping it by foot.

At Kristiansand Zoo, one session was conducted per day starting when the chimpanzees were allowed into the outdoor enclosure (approx. 8:30 am) and ending 3 hours later. Holes were reshaped to their original dimensions after each session. At Leintal Zoo, two sessions were conducted each day ($N_{\text{total}}=12$), the morning session starting at 9 am and the afternoon session starting around 12 pm. Sessions lasted between 1 and 5 hours depending on the daily routines of the chimpanzee keepers.

Unfortunately, the recordings of Session 5 were lost due a technical problem with the videocamera and therefore only 11 sessions were included in the analysis.

During the *Compacted soil condition*, the Kristiansand Zoo chimpanzees were provided with several disarticulated and defleshed horse (*Equus caballus*) bone fragments that could be used as excavating tools (see detailed measurements in Table S1). Bones were obtained from horse carcasses that were donated to the zoo for feeding their carnivores. In order to standardize the bone specimens that were then presented to the chimpanzees, we sawed the epiphyses from several horse humeri and femora and then, for some specimens, split their remaining diaphysie longitudinally with a saw. This standardization process allowed for easier cleaning of specimens prior to their introduction to the chimpanzees and also facilitated the measurement of potential quantitative changes in bone dimensions with chimpanzee use. All bone specimens were simmered for 90 min at 65° C in order to disinfect them before their introduction into the chimpanzee enclosures. Once simmered, any remaining soft tissues were removed manually from the bones and they were then measured. Mean starting bone fragments dimensions were (N=19): superoinferior length $\pm$ SD: 16.0 ± 4.28 cm, maximum width $\pm$ SD: 6.22 ± 0.93 cm, and weight $\pm$ SD: 308.94 ± 97.58 g. The bone fragments were provided to the chimpanzees by placing them in the study area next to the covered holes, flat on the ground.

The Kristiansand Zoo chimpanzees were provided with one to three horse bone specimens on a given day and each bone stayed with the chimpanzees for a period ranging between one and five days (Fig 1). This variation was due to the fact that although we aimed to recover each fragment after 24h, the chimpanzees often

271 hid/carried the bones with them between enclosures, preventing the experimenter
272 from recovering them. Furthermore, four of the bone fragments provided were lost,
273 presumably into the water-filled moat.

274
275 Figure 1: Four of the recovered horse humeri fragments provided to the chimpanzees
276 at Kristiansand zoo.

277
278 At Leintal Zoo, we provided the chimpanzees with four disarticulated, defleshed, and
279 simmered cow (*Bos taurus*) ribs (mean superoinferior length $\pm$ SD: 30.2 ± 1.19 cm;
280 mean maximum width $\pm$ SD: 4.02 ± 1.04 cm; mean weight $\pm$ SD: 125.75 ± 36.26 g)
281 cut at backbone (Fig 2). The number of ribs provided to the chimpanzees was limited
282 to four because those were the specimens available in the local butchery at the time of
283 the experiment. Before each session of the *Compacted soil condition*, we placed the
284 four ribs in the study area next to the holes and flat on the ground. Ribs were
285 recovered from the enclosure each day.

286

287 Chimpanzees participated in the experiment as a group. Recordings were made
288 everyday using one fixed camera (Sony HDR-CX330E Handycam) at Kristiansand
289 zoo and two cameras at Leintal zoo.

290

291

292 Figure 2: Top left: Baited hole from the *Open holes condition*. Top right: The four
293 cow ribs used in the *Compacted soil condition* at Leintal Zoo. Bottom left: Baited
294 hole in the *Loose soil condition*. Bottom right: Toto (hand-reared male, 37 years old)
295 in the first bone excavating event recorded during Session 2 of the *Compacted soil*
296 *condition* at Leintal Zoo.

297

298 *Coding*

299 In each session we coded all interactions between the chimpanzees and bone
300 specimens. An *event* was defined as each instance of a tool-related behaviour. The

duration of each tool-excavating event (when a chimpanzee used a tool to excavate) was calculated from the moment a chimpanzee introduced any part of a tool inside a hole until the chimpanzee extracted the tool from the hole. If the tool was abandoned inside the hole, the tool-excavating event ended when the chimpanzee released the tool. Individual chimpanzees were identified from video recordings.

Ethics

The experiments reported here comply with the Guide for the Care and Use of Laboratory Animals (National Research Council, 2011) and the American Society of Primatologists' Principles for the Ethical Treatment of Primates. This study was further approved by the ethical boards of Kristiansand Zoo and Leintal Zoo before its commencement. All participation in the study was voluntary and no isolation of individual subjects took place during the experiments. The experimenters never attempted to encourage the chimpanzees to interact or manipulate the testing materials. Subjects were never food nor water-deprived, and continued with their regular feeding routine during the study. Subjects had access to water ad libitum prior, during, and after testing.

Results

Raw data and sample video clips can be found in the OSF link:
https://osf.io/cewdz/?view_only=e9c48b3a63134e37a1f3032f5d7c74fa.

Kristiansand Zoo

The chimpanzees at Kristiansand Zoo were not observed excavating with the bones. However, they did interact with the bones in multiple other ways (Table 1). For

example chimpanzees were observed twice hitting bone specimens forcefully and repeatedly against a hard substrate (hammering), which led to the detachment of small bone fragments (see bottom right panel in Fig1 for an example) or to the fracture of the bone (see Fig S1). One adult male individual was observed on several occasions using a wooden skewer, employed by experimenters to mark the hole location in the study by Motes-Rodrigo et al. (2019), to pick and consume the marrow from the inside of several bones (see video in OSF). Bone throwing was observed when, on two separate occasions, a male threw a bone towards the camera across the moat while standing bipedally and piloerect as part of a display towards an unfamiliar human present in the observation point where the behavioural recordings were made from. Unfortunately, given that many of these interactions took place in the indoor enclosure (the chimpanzees transported the bones there) during the time the study area was being filmed, there are no recordings available from most of them.

Table 1: Ethogram of bone-related behavioural forms observed at Kristiansand Zoo. N represents number of observations. In those cases where N is preceded by > it means that the exact number of observations was not recorded and that N is an approximation.

Behaviour	Description	N
Tool-assisted marrow consumption	Holding the bone with one hand, a chimpanzee uses a skewer gripped by the other hand to perforate the exposed spongy bone of the medullary cavity either	3

	longitudinally or from one side, perpendicular to the longitudinal axis. Then, the skewer is retrieved and licked (see video in OSF link).	
Hammer	Holding the bone with one hand and in a sitting position, the chimpanzee hits a hard substrate (concrete) with it, fracturing the impacted surface of the bone.	2
Transport	The bone is carried from one place to another in two ways: 1) in the mouth pressing with the lips the middle part of the bone, or 2) inserting one of the ends of the bone in the oral cavity or holding it with a foot or a hand that is still used as support for locomotion.	>50
Monopolization	A chimpanzee takes the bone and places it close to his/her body while engaged in another activity such as feeding or resting. If another individual tries to take the bone, the owner places it closer to his/her body or out of reach from the other individual.	>30
Play	A chimpanzee places the bone on the ground and, sitting or standing, moves it along the substrate pressing it against the ground (like a	1

	toy car).
Throw	A chimpanzee holding the bone with one hand and in bipedal position, moves the arm backwards and then quickly forwards, throwing the bone away into the moat.

345

346 **Leintal Zoo**

347 *Bone-excavation events*

348 The chimpanzees at Leintal Zoo performed 180 behavioural events that involved the
 349 use of the cow ribs. Of these, 22 were bone-assisted excavating events (Table 2 and
 350 Table S2). The remaining events were non-excavating and these were classified as
 351 exploratory (133 events including sniff and mouth), social (display: 8, hit other: 1),
 352 and transport (16) (Table 1 and Table S1).

353

354 Table 2: Ethogram of bone-related behavioural forms observed at Leintal Zoo.
 355 Excavating behaviours are defined following Motes-Rodrigo et al. (2019).

356

Behaviour	Description
Dig	A chimpanzee holds a bone tool with one or two hands and places it into the ground. Then, while pressing the tool in the ground, moves it towards the edge of the hole, which produces the extraction of soil from the hole.

Perforate	A chimpanzee inserts a tool perpendicular to the ground and applies force pushing the end of the bone into the ground with one or more extremities. Power grip is used if one of the hands holds the midsection of the bone. The bone is then retrieved and the end that went into the ground may or may not be visually and olfactorily inspected. No soil is displaced from the hole.
Pound	A chimpanzee holds the bone with one or both hands and with powerful up and down movements of the tool hits the ground repeatedly in a stabbing motion. No soil is displaced from the hole.
Probe	A chimpanzee holds one end of a bone and places the other end in a hole exerting light pressure or performing small wrist movements. The bone is then withdrawn and the inserted end may or may not be visually and olfactorily inspected. No soil is displaced from the hole.
Hold	A chimpanzee holds the bone with a hand or a foot
Sniff	A chimpanzee brings the bone close to the nose and sniffs it.
Mouth	A chimpanzee shortly puts the bone inside the mouth.

Display A chimpanzee uses the bone as part of a display
 hitting the ground or shaking it in the air, which
 causes the chimpanzees around him to move away.

Attempt to A chimpanzee tries to hit another chimpanzee with
hit other the tool.

Transport A chimpanzee moves to another location while
 carrying the bone on the hand, foot or mouth.

357

358 The first bone excavating behavioural form was observed on the 5th of October 2018
359 by Toto (human-reared, male, 37 years old), who performed the behavioural form
360 *bone probe* (for 2 seconds) for the first time at 00:02:54 in session 2 of the
361 *Compacted soil condition* before proceeding to excavate manually (bottom right panel
362 of Fig 2, Table S2). Also in session 2, Toto performed for the first time the
363 behavioural forms *bone perforate* and *bone pound*. By session 12, eight different
364 individuals (two human-reared and six mother-reared) had manipulated the bones in
365 the context of excavation (Table S2). The six mother-reared individuals that used
366 bones only performed the behavioural form *bone probe* (Table S2), while all other
367 bone related behavioural forms were performed by Toto (10/22 events: dig, pound,
368 perforate) and Panya (human-reared, female, 11 years old, 2/22 events: pound, dig).

369

370 The bone tool excavation events lasted on average 6.45 ± 5.28 seconds (range 1-26
371 seconds). None of the bone tool excavating events led by itself to the retrieval of the
372 buried food items. In some cases, the food had already been dug out by another
373 individual before excavation with bones occurred. In the cases where food was still

present, the apple was never obtained as a direct consequence of using a bone. Instead, the apples were always obtained by manual digging, but the use of bones seemingly aided in some cases to obtain the apples by loosening the soil and thus facilitating subsequent manual excavation. In 16 bone-excavating events it was possible to determine in which part of the excavation sequence bones were used. Bone-related excavation in a given hole occurred before (N=4), after (N=8) or between (N=4) manual excavation events in that same hole by a given individual.

Reuse of bone tools left inside holes

On seven occasions, bones were left inside the holes (with one end of the bone at the bottom of the hole). In one of these occasions, the same individual reused the bone (13 seconds after leaving the bone). In six of these occasions, a different individual from the one who left the bone in the hole retrieved the bone. Based on these observations, we analyzed how the individuals that found bones within the holes interacted with them. Only one individual (Panya) used bones (N=2) she found inside holes for excavating in two occasions (session 2). In two other cases the arriving chimpanzee took the bone out of the hole, held it, sniffed it, and put it on the floor outside the hole (once in session 1, once in session 2). On the three remaining occasions (once in session 1, once in session 8 and once in session 12), the bone was taken out of the hole and placed on the ground without previously performing any other action.

Discussion

Our study represents the first description of the behavioural responses of captive chimpanzees to disarticulated bones in the context of food excavation. We found that

chimpanzees in one population used cow ribs to aid in excavation when these materials were readily available in the proximity of buried food. The chimpanzees that engaged in bone-assisted excavation had never been exposed to bones before the present study and had only anecdotal experience with underground food items (i.e. naturally occurring insects and buried juice bottles where the chimpanzees could dip in with tools). In contrast, the chimpanzee population that did not engage in bone-assisted excavation had ample experience with stick-assisted excavation from a previous experimental study. Thus, previous experience in tool-excavating tasks did not predict the use of bones by subjects during the current excavation experiment.

In a previous study on plant tool excavation conducted with the Kristiansand chimpanzee population, we found that tool length was the only tool characteristic that influenced the probability that the chimpanzees used a plant tool over other types of provided potential plant tools to excavate (Motes-Rodrigo et al., 2019). The length range of the sticks selected and used as excavating tools in our previous study was 28-57.5 cm (Table 5 in Motes-Rodrigo et al., 2019). The length of the bones provided to the Kristiansand chimpanzees in the present study was outside this range (12-20 cm), whereas the bones provided to the Leintal chimpanzees were within the range of the plant tools previously used to excavate by the Kristiansand chimpanzees (29-31 cm). Furthermore, bone weight also differed between the materials provided to each of the chimpanzee groups, with the bone materials provided to the Kristiansand chimpanzees being twice as heavy on average than the bone materials provided to the Leintal chimpanzees. The fact that the Kristiansand chimpanzees never used any of these bones as excavating tools, despite being familiar with tool-assisted excavation of buried food items, suggests that the chimpanzees did not perceive these bones as

suitable tools for the task (the bones might have been too short or too heavy to be effective or to hold comfortably as excavating tools). This lack of suitability could have also been influenced by the fact that the epiphysis of the bones had been removed and some of the bones had been split open along their long axis, exposing the cancellous tissue and the bone marrow. The exposure of the endosteal bone surfaces, with adhering residual marrow, which is edible and nutritious, might have distracted the chimpanzees from using the bones as excavating tools. Based on our observations from two different chimpanzee populations with different experience in excavating tasks, we hypothesize that it is object dimensions, rather than raw material type, that determines whether chimpanzees will use an object as a tool to excavate or not.

The observations that we made in Leintal of bone-assisted excavation involved several actions similar to those described in the context of stick-tool excavation (Motes-Rodrigo et al., 2019). However, Leintal chimpanzees engaged in much shorter bouts of bone excavation, as compared to plant tool excavation previously observed among the the Kristiansand chimpanzees [1-26 seconds in Leintal compared to 2-254 seconds in Kristiansand, although it is important to take into consideration the differences in number of events observed by Motes-Rodrigo et al., (2019) (>300) and this study (22)]. Given the stable provision of food in captive settings and the fact that the chimpanzees combined bone excavation with manual excavation, our results suggest that the use of bones as tools by the Leintal chimpanzees was opportunistic rather than a necessity. The combination of manual and tool excavation by these chimpanzees suggests that in our experimental set-up the use of bones did not provide a sufficient advantage over manual excavation for the chimpanzees to exclusively

excavate using tools (see also the relative profitability hypothesis by Rutz & St Clair, 2012).

Contrary to the Leintal chimpanzees, the chimpanzees housed at Kristiansand zoo, who had extensive prior experience in plant tool-excavation, did not use the provided bones as excavating tools. Instead, these chimpanzees performed other behaviours not observed in the Leintal population such as using bones as hammers and consuming marrow by extracting it from the bones with a skewer (see video in OSF link). This later behaviour (stick-assisted marrow consumption) was likely elicited in Kristiansand zoo but absent in Leintal zoo as a consequence of the differing characteristics of the bones provided in each institution. In Kristiansand zoo the bone grease and marrow was exposed in the metaphyses of the bones as a result of the epiphyses being removed previously by experimenters. In addition, some bones were cut longitudinally exposing the bone marrow in the diaphysis as well. The accessibility of bone marrow could have then elicited marrow consumption in the Kristiansand chimpanzees. Leintal chimpanzees however, were provided with complete bones without any exposed bone marrow.

Given that chimpanzees have been shown to use tools of several different materials to excavate (bones, sticks, skewers, plastic tubes; Motes-Rodrigo et al., 2019; this study), it seems that the same excavating behavioural forms can be flexibly exhibited regardless of the tool material. The differing results that we obtained from two chimpanzee populations with varying degree of excavating proficiency, suggest that the shape or functional properties (rigidity, length, and thickness) instead of the tool material itself determine if an object can be used as an excavating tool. These results

are comparable to those of previous studies reporting that when engaging in multiple foraging behaviours, chimpanzees choose and use objects as tools based on the physical characteristics of those objects (Boesch & Boesch, 1983; Carvalho et al., 2008; Lamon et al., 2018; Seed et al., 2012; Sirianni et al., 2015).

Our study might have been limited by the modest number of bones that we provided to each group of chimpanzees and the impossibility of performing a crossed-factor experimental design. The number of bones provided in Kristiansand zoo was determined by the availability of privately own horses donated to the zoo. At Leintal zoo the number of cow ribs available was determined by the cow-butcherer schedule of the town where the experiments were conducted. The low number of bones provided at each site also meant that high-ranking individuals often monopolized the bones or excavating sites, limiting the access of the rest of the individuals to the study area and materials. Ideally, each population of chimpanzees would have been provided with multiple bones of varying characteristics. However, this was not possible in the present study due to resource and time constraints.

It is also worth noting that the two chimpanzees that engaged in bone-excavating behaviors other than probing, had both spent time as infants in the care of humans. However, it seems unlikely that rearing conditions alone could explain the performance of the Leintal chimpanzees given that there was a human-reared chimpanzee in Kristiansand zoo who did not use the bones to excavate as well as six other human-reared chimpanzees at Leintal zoo that did not interact with the bones. Future studies may wish to further investigate if and how the rearing background of

chimpanzees interacts with bone characteristics in influencing the emergence of bone-assisted excavation.

Despite these potential limitations, the observations collected in both Kristiansand and Leintal zoo represent some of the first observations on the spontaneous behavioural responses of captive chimpanzees towards bones (see also Pickering & Wallis, 1997). The data from the excavating-savvy chimpanzees of Kristiansand zoo is particularly interesting in this regard, as the bones were not employed to access buried foods (perhaps due to their physical characteristics as mentioned above). The bone-related behaviours reported from the Kristiansand chimpanzees provide important preliminary data on some of the behaviours that early hominins might have engaged with (which may or may have not led to surface modifications). Wear marks and surface modifications on archaeological artefacts are often associated inferentially with different foraging behaviours (e.g., Brain et al., 1988; Backwell & d’Errico, 2001; d’Errico & Backwell, 2009), but our results open different possible avenues for the use of bones by early hominins. Hammering, throwing and potentially playing with bones as observed in the chimpanzees of our study might have also been present in the behavioural repertoire of our hominin ancestors.

The findings presented here show that certain chimpanzees can use bones to assist in the excavation of buried food items. Based on our results, we hypothesize that object dimensions are an important determinant of whether an object is used as an excavating tool. The hypothesis that material properties play an important role in determining the functionality of potential tools is supported by the homogeneous physical characteristics of the bone tools found in the archaeological record (Backwell

& d’Errico, 2001; d’Errico & Backwell, 2009). Within the framework of primate archaeology, our study represents a first attempt to gain insight into the behaviours that preceded, as well as the initial stages of bone technologies using apes as models for early hominin behaviour. As a proof of concept, our findings show that chimpanzee studies can be used to assess multiple aspects of the early emergence of bone technologies much as this species has been used to better understand the archaeology of perishable plant tools potentially used by early hominins (Almeida-Warren et al., 2017; Pascual-Garrido, 2018; Pascual-Garrido & Almeida-Warren, 2021). We hope that our study serves to foster novel primate archaeological research investigating aspects of bone technologies such as the learning mechanisms underlying the acquisition of bone-related behaviours, surface-wear analysis of primate-used bone tools and bone tool modifications.

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Appendix

Keeper reports

The keepers at Leintal zoo reported that the chimpanzees had been observed several times, since the summer of 2018, "scratching soil" (as defined by the keepers: "using wooden sticks on the ground") in the area surrounding a climbing pole in the outdoor enclosure. The keepers speculated that the chimpanzees might have been looking for or feeding on insects, or simply playing with dirt (the keepers reported that it is a common behavior in this group to collect loose dirt by hand and throw it at other individuals, a behaviour also observed by the experimenter). However, no recordings of these episodes were available and no more detailed descriptions of the behavior could be obtained.

On one occasion in 2017, a plastic bottle filled with juice was buried by the keepers head up and without a cap in the outdoor enclosure of the chimpanzees to motivate them to dip in the juice with sticks. The keepers reported that after some time dipping sticks in the bottle and sucking the juice from the sticks the chimpanzees dug up the bottle (this was not measured so the duration of these events is not available). However, no recordings of how the bottle was extracted were made and therefore it is not possible to know if the chimpanzees used tools in the process or simply pulled up the bottle by gripping or biting its head. Crucially, all three keepers confirmed that none of the chimpanzees had ever had any previous experience with bones (nor bone tools).

Supplementary table 1: Measurements and characteristics of the horse bones provided to the chimpanzees at Kristiansand zoo. Length refers to the maximum length of the longest axis of the bone. Max width refers to the maximum width of the bone. Columns 5 to 8 refer to the angle measurements of the four bone ends from which the epiphysis had been removed. These angles were measured with a goniometer by placing one arm on the periosteal surface of the bone and the other arm on the sawed apical surface. Bone type refers to the bone from which the bone fragments were created. F means horse femur and H means horse humerus.

Tool nr	Days of use	Length (cm)	Max width (cm)	Angle left top	Angle right top	Angle left bottom	Angle right bottom	Weight (g)	Bone type
1	5	18.6	6.6	98	94	97	98	354	F
2	5	14.2	7,2*	118	65	90	96	496	F
3	5	15	8	94	97	82	104	270	F
4	1	14.58	5.8	95	104	92	94	270	F
5	1	11.7	5.9	117	90	89	89	210	F
6	1	11.1	5.9	91	101	89	61	178	F
7	1	15.4	6	106	95	92	91	264	F
8	1	7.8	6.8	5.9*	72	6.8*	88	204	H
9	1	7.5	8.6	6.6*	90	8.5*	90	264	H
10	2	17	6.1	74	98	87	93	222	H

11	NA	16.3	5.2	95	96	76	95	276	H
12	2	18.1	5.5	93	100	79	94	290	H
13	2	18.5	5.6	100	98	93	80	320	H
14	1	19.5	6.8	115	83	82	90	340	H
15	NA	19.6	6.9	111	81	81	91	336	H
16	2	17.6	5	85	93	97	75	256	H
17	NA	17.6	5.4	96	89	76	97	416	H
18	NA	22.6	6.1	103	92	94	97	344	H
19	NA	23	5.8	92	105	82	95	560	H

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728 Supplementary Table 2: Bone excavating events recorded. Order indicates the use of
 729 bones relative to manual excavation events (before: before excavating manually;
 730 after: after excavating manually; between: between manual excavation events). L=
 731 left hand, B =both hands, F=foot, R=right hand, RF=right foot.

Session	Date	Time of day	Start	End	Duration (sec)	Individual	Rearing history	Action	Hand	Order
2	5.10.18	afternoon	00:02:54	00:02:56	2	Toto	human	probe	L	before
2	5.10.18	afternoon	00:05:15	00:05:23	8	Donald	mother	probe	L	NA
2	5.10.18	afternoon	00:08:05	00:08:09	4	Toto	human	pound	R	after
2	5.10.18	afternoon	00:09:01	00:09:11	10	Toto	human	perforate	BF	before
2	5.10.18	afternoon	00:10:43	00:10:55	12	Toto	human	perforate	BF	after
2	5.10.18	afternoon	01:06:42	01:06:44	2	Girlie	mother	probe	L	after
2	5.10.18	afternoon	00:00:08	00:00:10	2	Panya	human	probe	L	NA
2	5.10.18	afternoon	00:00:11	00:00:20	9	Panya	human	probe	L	NA
2	5.10.18	afternoon	00:01:11	00:01:12	1	Zicklein	mother	probe	R	NA
2	5.10.18	afternoon	00:02:07	00:02:12	5	Panya	human	pound	R	before
2	5.10.18	afternoon	00:02:12	00:02:21	9	Panya	human	dig	R	before
2	7.10.18	afternoon	00:03:08	00:03:12	4	Panya	human	probe	L	between
6	7.10.18	afternoon	00:00:00	00:00:08	8	Toto	human	perforate	RF	NA
6	7.10.18	afternoon	00:00:09	00:00:13	4	Toto	human	pound	R	NA
7	8.10.18	morning	00:29:01	00:29:09	8	Garibal	mother	probe	R	after
8	8.10.18	afternoon	01:32:22	01:32:27	5	Toto	human	probe	R	after
8	8.10.18	afternoon	01:37:50	01:37:54	4	Girlie	mother	probe	L	after
8	8.10.18	afternoon	01:38:20	01:38:26	6	Toto	human	perforate	LF	after
10	9.10.18	afternoon	01:26:57	01:27:02	5	Toto	human	dig	R	between
10	9.10.18	afternoon	01:36:30	01:36:56	26	Lutz	mother	probe	B	between
12	10.10.18	afternoon	02:22:26	02:22:28	2	Donald	mother	probe	L	after
12	10.10.18	afternoon	02:24:07	02:24:13	6	Schon	mother	probe	L	between

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735 Supplementary Figure 1: Four examples of fragmented bones that were recovered
736 from the chimpanzee enclosures.

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